ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

SILVESTRIA 176

Responses of *Bupalus piniarius* to Plant Quality Variation Generated by Larval Feeding

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Akademisk avhandling som för vinnande av filosofie doktorsexamen kommer att offentligen försvaras i hörsal L, SLU, Ultuna, fredagen den 23 mars 2001, kl. 9.30.

Abstract

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B. piniarius prefers to feed on mature Scots pine (*Pinus sylvestris*) needles throughout the larval period. Depletion of the preferred resource caused by defoliation negatively affected larval performance, *i.e.* larvae on current-year needles suffered higher mortality and resulted in lighter pupae than conspecifics on branches containing both current-year and mature needles. There was no support for the induced resistance hypothesis. On the contrary, larvae feeding on previously defoliated branches performed better than those feeding on non-defoliated branches suggesting induced host susceptibility. Crowding associated with high population densities enhanced larval performance.

Ovipositing females showed a distinct preference for mature needles. When confined to current-year needles, females responded with reduced realised fecundity and frequently placed their eggs in an unsafe manner, *i.e.* on needle scales and stacked in several layers on top of each other. Due to their misplacement some eggs fell off the plant. Only a small fraction of larvae hatching from eggs on the ground was able to recolonise the host tree.

In order to estimate possible errors in forecasts of *B. piniarius* population changes due to random weather events, effects of low temperature and delayed mating on realised fecundity were studied in the laboratory. At 10 °C *B. piniarius* oviposition was almost completely arrested. Females that experienced 10 °C for four days had lower fecundity and increased longevity compared with females raised at constant 20 °C. Four days delayed mating at 20 °C had no effect on fecundity but affected fertility, *i.e.* 30% of eggs were laid before mating.

It is concluded that defoliation-mediated variation in host plant quality can significantly influence *B. piniarius* population dynamics under outbreak conditions.

Key words: defoliation, egg loss, growth rate, insect outbreaks, insect – plant relationship, mutual interference, population behaviour, realised fecundity, recolonisation.

Distribution:
Swedish University of Agricultural Sciences
Department of Entomology
S-750 07 UPPSALA, Sweden

Uppsala 2001
ISSN 1401-6230
ISBN 91-576-6060-3

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Tryck: SLU Service/Repro, Uppsala 2001

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Šmits, A. 2001. Responses of *Bupalus piniarius* to plant quality variation generated by larval feeding. Doctor's dissertation.
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Contents

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals.

I. Šmits, A. Performance of pine looper *Bupalus piniarius* larvae under population build-up conditions. Manuscript.

II. Šmits, A. & Larsson, S. (1999) Effects of previous defoliation on pine looper larval performance. *Agricultural and forest entomology 1*, 19-26.

III. Šmits, A., Larsson, S. & Hopkins, R. (2001) Reduced realised fecundity in the pine looper *Bupalus piniarius* caused by host plant defoliation. *Ecological entomology*. In press.

IV. Šmits, A. Effects of low temperature and delayed mating on pine looper (*Bupalus piniarius*) fecundity. Manuscript.

Introduction

The reasons why some insect populations frequently reach outbreak levels, while other populations are characterised by stable dynamics have long been of interest for ecologists. Populations of foliage-feeding forest insects have often served as model systems when this question has been investigated because long term data series are available (Barbosa & Schultz, 1987; Hanski, 1987; Wallner, 1987; Berryman, 1988; Larsson *et al.*, 1993; Price, 1994; Cappuccino & Price, 1995). In addition to being of theoretical interest, knowledge about the mechanisms that drive population fluctuations are of great importance in applied ecology. For example, monitoring and forecasting population dynamics are essential parts of integrated pest management in forestry and agriculture (Way & van Emden, 2000).

Ecological studies increasingly focus on population behaviour (*e.g.* population cycles) (Liebhold & Kamata, 2000). In general, factors that contribute to insect population cycles can be divided into three major groups – weather, natural enemies, and host plant quality. Studies on natural enemies and weather have a long history (*e.g.* Wallner, 1987; Kidd & Jervis, 1997, and references therein). In the last few decades, however, more attention has been paid to host plant quality and quantity (*e.g.* Tallamy & Raupp, 1991; Haukioja & Honkanen, 1997; Karban & Baldwin, 1997).

The quality of the plant as food for insect herbivores is determined by its nutritional value as well as its defensive properties, such as toxicity and mechanical obstacles (*e.g.* Karban & Baldwin, 1997). Because of large variability in host plant characteristics insect herbivores show distinct preferences for particular plant species, particular individuals, or age of plant tissue (Bernays & Chapman, 1994). Outbreaks of some insect species occasionally result in complete or partial depletion of resources leaving insects with limited choices (*e.g.* Day & Leather, 1997). Although shoots of defoliated plants usually have regrowth capacity (Ostaff & MacLean, 1995; Krause & Raffa, 1996) the chemical composition of new leaves may differ from normal leaves (*e.g.* Tallamy & Raupp, 1991). Future generations of insects feeding on defoliated plants may show lower performance, *e.g.* survival and fecundity (*e.g.* Haukioja & Niemelä, 1977, Shultz & Baldwin, 1982). Decreased insect performance on previously defoliated plants, often referred to as induced plant resistance (Haukioja & Honkanen, 1997), can affect insect population dynamics (*e.g.* Haukioja, 1990, Karban & Baldwin, 1997). Defoliation may, on the other hand, result in improved food quality. Such herbivore-triggered susceptibility can potentially result in positive feedback to population dynamics of herbivorous insects (*cf.* Ruohomäki *et al.*, 2000).

The aim of this thesis was to study effects of variable resource quality, associated with high insect population densities on survival and reproduction of *Bupalus*

piniarius L. (Lepidoptera, Geometridae). Although three papers included in this thesis deal with effects of defoliation, each of them looks at the processes during one particular phase of an outbreak (Fig. 1). Paper I was intended to simulate the early phase of an outbreak with depletion of mature needles occurring in late larval instars. At this phase high population densities (crowding) are thought to cause mutual interference among larvae (Klomp & Gruys, 1965, Gruys, 1971). However, because no defoliation occurred in the previous year, no delayed induced responses in the host plant would be present at this phase. Paper II and III deal with a later phase of an outbreak when larvae and adults are forced to utilise the less preferred current-year needles on previously defoliated trees because of severe defoliation in the previous year. Paper II focuses on effects of delayed induced responses of the host plant on larval performance. Effects of previous defoliation on female preference and performance were studied in paper III. As in paper II, *B. piniarius* was confined to current-year needles of previously defoliated trees. However, this study focused on recruitment success in the absence of preferred resources. In paper IV, I tried to understand the importance of random weather events. This study is not associated with peak *B. piniarius* densities, but estimates possible errors in decision making by forest managers during the outbreaks.

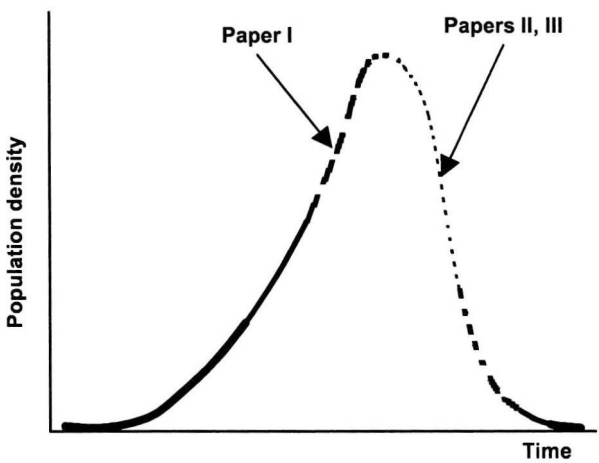

Fig. 1. Hypothetical *Bupalus piniarius* population cycle showing timing of effects studied in different papers included in this thesis. Thickness of the line corresponds to host defoliation, *i.e.* bold solid line corresponds to full foliage, and thin dashed line to heavy defoliation.

Population ecology of *Bupalus piniarius*

Life-cycle

The pine looper moth *Bupalus piniarius* is a univoltine insect that is monophagous on pine *Pinus* spp. In Sweden, adults emerge in June-July, copulate in the pine canopy and soon afterwards start to lay eggs in rows on the needle surface. Males emerge one to two days before females (Botterweg, 1982).

*F*ecundity closely correlates with pupal weight (Bevan & Parmonov, 1961), and usually one female lays 90 to 150 eggs (Bevan & Brown, 1978). Adults do not feed. They live for two to three weeks. Females are poor flyers and do not migrate more than 150 m throughout their lifetime (Botterweg, 1978). Egg development lasts two to three weeks. The larval period lasts three to four months, during which larvae pass through four to six instars. Larvae feed on pine needles but during outbreaks, when pine trees are completely defoliated, larvae may feed on other plants such as Norway spruce (*Picea abies*) and heather (*Calluna vulgaris*). Larvae descend to the ground in October-November, pupate in the soil, and overwinter as pupae.

Economic importance

Bupalus piniarius has long been recognised as a serious forest pest. Outbreaks have been recorded throughout Europe and Siberia (*e.g.* Schwerdtfeger, 1941; Butovitsch, 1946; Kondakov & Sorokopud, 1982; Broekhuizen *et al.*, 1993). Especially harmful outbreaks have occured in Germany (Escherich, 1931; Ebert, 1967; Klimatzek, 1972, 1979; Varley, 1949). Although outbreaks of *B. piniarius* characteristically occur in Scots pine (*Pinus sylvestris*) stands, high densities have also been observed in plantations of Corsican pine (*P. nigra*) and lodgepole pine (*P. contorta*) (Barbour, 1988). Even a slight defoliation may reduce tree growth for several years (Straw, 1996). Severely defoliated stands often suffer high tree mortality due to subsequent infestation by the bark beetle *Tomicus piniperda* (*e.g.* Crooke, 1959), especially if defoliation occurs during two successive years (Schwenke, 1978). Due to its high economic importance *B. piniarius* has been intensively studied. Several life-tables are available (Klomp, 1966; Broekhuizen *et al.*, 1994; Marchenko, 1994). The most detailed ecological studies have been carried out in the Netherlands and in the United Kingdom (Bevan & Parmonov, 1961; Klomp, 1966, Gruys, 1970; Botterweg, 1978; Broekhuizen *et al.* 1993, 1994).

Population behaviour

Many *Bupalus piniarius* populations show distinct cyclic dynamics (*e.g.* Varley, 1949; Klomp, 1966; Barbour, 1988, 1990). Several possible mechanisms underlying population dynamics have been proposed. Ginsburg and Taneyhill (1994) suggested that cyclicity in *B. piniarius* populations might be caused by intrinsic factors, *i.e.* maternal effects. However, most theories about *B. piniarius* population behaviour consider extrinsic factors. Klomp and Gruys (1965) and Gruys (1971) argued that mutual interference between larvae, acting in a density dependent manner, may be regulating *B. piniarius* populations. In contrast, Barbour (1988) suggested that larval and pupal parasitism is the main force causing population cycles. More than 60 parasitoid species are known to attack *B. piniarius* (Schwenke, 1978), although only a few species are abundant. Among ichneumonid species *Cratichneumon viator* is considered to be of particular

importance (Urban, 1966; Haeselbarth, 1979a, 1979b; Õunap, 1996). It attacks pupae in the autumn soon after *B. piniarius* larvae have descended from the canopy and also in early spring when newly emerged parasitoids attack pupae not parasitised in the autumn. Up to 75% of the parasitism can be caused by this second parasitoid generation (Davies, 1962). Other important parasitoids are the ichneumonid *Poecilostictus cothurnatus* and the tachinid *Eucarcelia rutilla* (Schoonhoven, 1962; Herrebout, 1966, 1969; Van Veen, 1981). Although many parasitoid species seem to attack *B. piniarius* at endemic population densities, high parasitism rates occur only when high density population are declining (Barbour, 1988). Similarly, cytoplasmic polyhedrosis virus can significantly contribute to population decline (Jahn & Sinreich, 1957). The impact of natural enemies on population dynamics works in a delayed density-dependent manner, and new population increase is possible after relaxation of this pressure (Barbour, 1988).

Climatic conditions are considered to be important in the formation of outbreaks. Most frequently, outbreaks occur in rather warm and dry areas with annual rainfall of 500 to 600 mm (Schwenke, 1978; Broekhuizen *et al.*, 1993). Due to the long larval development early autumn frosts may prevent larvae from pupating and thus contribute to overall population decline (Marchenko, 1994). The fact that *B. piniarius* development is favoured by drought may indicate that stressed trees are more susceptible than non-stressed trees (*e.g.* Larsson & Tenow, 1984). However, little is known about the role of host plant quality in *B. piniarius* dynamics. Miller *et al.* (1977) showed that nitrogen content in pine foliage increases after defoliation by *B. piniarius*. Consequently, *B. piniarius* could take advantage of elevated nitrogen concentrations. However, pupal weight tends to decline after peak densities (Barbour, 1988).

Most probably, *B. piniarius* population dynamics are driven by a combination of factors. Dempster (1975), based on the key factor analysis provided by Klomp (1966), concluded that no single factor can be identified as always important. More detailed analyses of the same data by Royama (1997) revealed that factors damping cycles are acting in early and late larval stages and during the egg stage.

Results and discussion

Larval performance

Larval performance on non-preferred resources

As a first step to assess the role of host plant quality for *Bupalus piniarius* growth and survival larval feeding preferences were studied. Although larvae feed on all age classes of Scots pine needles, a more careful survey revealed a distinct larval

preference for mature needles (II). A more than three-fold difference in damage was found between mature and current-year needles. Earlier observations indicate that late instar *B. piniarius* larvae largely feed on current-year needles (Broekhuizen *et al.*, 1993; Straw, 1996). These observations were probably from high-density populations where larvae had little choice. However, in the present study larvae always had a choice between young and mature needles. Thus, in a choice situation late instar larvae do prefer mature needles. Generally, plants invest more in defence of young tissues (McKey, 1979). For instance, in Scots pine terpenoids are present in higher concentrations in current-year needles than in mature needles (Ikeda *et al.*, 1977; Niemelä *et al.*, 1982). Thus, the observed preference for mature needles in *B. piniarius* may be explained by a higher toxicity of current-year needles.

The hypothesis that current-year needles are a suboptimal resource for larval development was tested in laboratory and field experiments (I, II). Both young and late-instar larvae showed lower performance on branches bearing only current-year needles than conspecifics on control branches containing shoots with both mature and current-year needles. Larvae feeding on the less preferred current-year shoots suffered higher mortality. This was more pronounced for late instars (I) than early instars (II), although differences could be attributed to the different experimental conditions; young larvae were grown on cut branches (II) while late-instar larvae were placed in sleeve cages on living trees (I). Larvae feeding on current-year needles also resulted in lighter pupae (corresponding to lower potential fecundity) than larvae feeding on control branches. These results support the hypothesis that current-year needles are a suboptimal resource for larval performance.

At high population densities, when pine trees are completely defoliated, *B. piniarius* larvae feed on plants that are not normally accepted as hosts (*e.g.* Norway spruce, heather). Experiments with late instar larvae showed that although some larvae were able to complete development on Norway spruce the costs for feeding on this resource were high (I). There was 82% reduction in survival, reduction in pupal weight corresponding to 80% reduction in potential fecundity, and a significantly prolonged development.

Constitutive plant defences and induced susceptibility

In addition to depletion of the preferred resource, larval defoliation may also induce changes in foliage chemistry that can have negative effects on larval performance (*e.g.* Haukioja & Honkanen, 1997). The induced resistance hypothesis was tested in laboratory and field experiments at Hökensås, in southern Sweden where an extensive outbreak of *B. piniarius* occurred in 1996 (II). Larval survival on current-year needles from non-defoliated trees did not differ from that on shoots taken from trees defoliated the previous year (in the following referred to as defoliated shoots; also note that only current-year

needles are available the year following a complete defoliation). Furthermore, larvae on non-defoliated shoots showed a reduced growth rate compared to those on previously defoliated shoots.

Interestingly, consumption rate on non-defoliated current-year needles was significantly higher than on defoliated shoots indicating that although larvae on non-defoliated shoots consumed more needle tissue they grew slower. This suggests that non-defoliated current-year shoots contain more toxic compounds than defoliated shoots. Larvae may spend more resources for detoxification, or defoliated shoots may have increased nutritional value for larvae compared with non-defoliated. The second possibility was supported by nitrogen data; needles on defoliated branches contained more nitrogen than those on non-defoliated. Such an increase in nitrogen content after *B. piniarius* defoliation has also been recorded by Miller *et al.* (1977).

Other evidence of defoliation-induced host plant susceptibility was obtained from the field experiment (II) where larvae were reared on naturally defoliated trees and non-defoliated trees. Although larvae on non-defoliated trees had access to preferred mature needles pupae from these larvae were 22% lighter than pupae from defoliated trees. However, in this experiment it was not possible to fully separate an effect of food quality from possible effects of differences in microhabitat; defoliated trees were more exposed to the sun because foliage was scarce.

I concluded that complete defoliation caused by *B. piniarius* larvae did not trigger delayed induced **resistance** in Scots pine. Defoliation rather tended to increase host plant **susceptibility**. Similar induced susceptibility has been shown for pine sawflies (Niemelä *et al.*, 1984, 1991). In contrast, defoliation-induced resistance has been found in another pine-feeding insect *Panolis flammea* (Trewhella *et al.*, 1997). The differences in responses of particular insects to induction may depend on herbivore feeding behaviour. *P. flammea* initially feeds on current-year needles whereas the pine sawflies and *B. piniarius* initially feed on mature needles. In fact, the European pine sawfly *Neodiprion sertifer* prefers to feed on previously defoliated branches (Trewhella *et al.*, 1997).

Crowding effects

Outbreaks of folivorous insects are associated not only with defoliation, and thus competition for food, but also with crowding that may result in competition for space. Mutual interference is thought to be important in damping *B. piniarius* population cycles (Klomp & Gruys, 1965). Based on the study by Gruys (1970) that showed significant negative effects of low-level crowding on larval performance, it was hypothesised that crowding will have negative effects on *B. piniarius* larval performance.

Laboratory and field experiments with late-instar larvae, however, revealed that crowding enhanced rather than suppressed larval development (I). Larvae grown in cohorts of ten grew faster than solitary larvae, and reached the same pupal weight with shorter development time. The higher growth rate of crowded larvae was probably achieved by increased consumption rate, as indicated by increased faeces production.

Although facilitated growth rate of crowded larvae has been recorded in other insects (Hill & Hirai, 1986; Haukioja *et al.*, 1988; Goulson & Cory, 1995) the results of this study obviously contradict Gruys' (1970) results. The difference could be attributed to differences in experimental design. First, most of Gruys' experiments used young larvae, whereas larvae in late instars were used in this study. Second, in Gruys' study larvae were reared on non-preferred current-year needles. Third, and probably most important, there was a difference in crowding level. Gruys used two to five larvae per cohort whereas in this study groups of ten larvae were used to simulate crowding conditions. The last argument suggests a non-linear relationship between crowding level and growth rate, sometimes found for other insects (*e.g.* Danthanarayana *et al.*, 1982; Goulson & Cory, 1995). Although fast development at certain circumstances is advantageous, there are costs associated with it, *e.g.* increased susceptibility to diseases (Goulson & Cory, 1995; Fuxa *et al.*, 1999).

There was no interaction between effects of larval crowding and feeding on non-preferred resources (I). However, the two factors worked in opposite directions. Larval crowding enhanced larval development whereas feeding on non-preferred current-year needles had negative effects on larval performance.

Fecundity as related to resource quality

The next logical step to assess the role of resource quality is to look for effects of defoliation on recruitment success. By recruitment I mean realised fecundity and successful egg conversion into larvae (*e.g.* Royama, 1997). The success of larval development is largely determined by ovipositing females who choose development sites. Most often preference for oviposition is positively associated with offspring performance (for review see Thompson & Pellmyr, 1991), although, low preference does not always lead to reduced performance (*e.g.* Pasquier-Barre *et al.*, 2000).

Oviposition preferences

The distribution of *Bupalus piniarius* eggs was surveyed in the field (III) on branches with different levels of defoliation. Although eggs were found on all needle types many more eggs were found on mature needles than on current-year needles (Fig. 2). The differences between needle age classes were especially pronounced on heavily defoliated branches where the few remaining mature

needles were usually used for egg deposition. Even dry needles damaged by previous larval feeding were commonly used for egg deposition (Fig. 3).

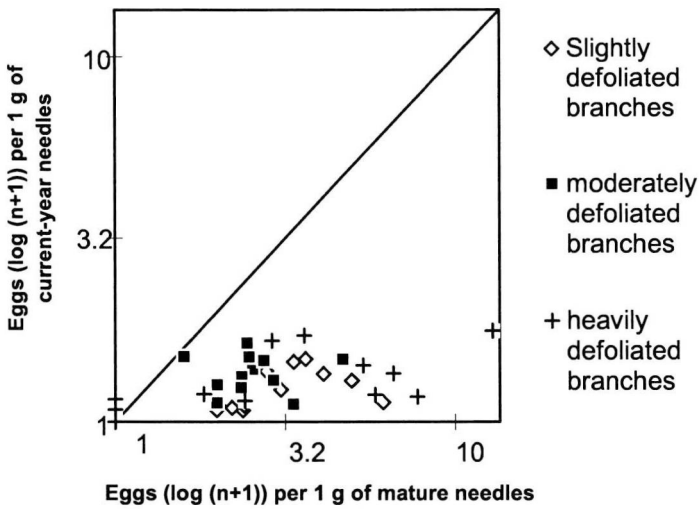

Fig. 2. Number of *Bupalus piniarius* eggs found on the mature and current-year needles in Scots pine branches with different levels of infestation.

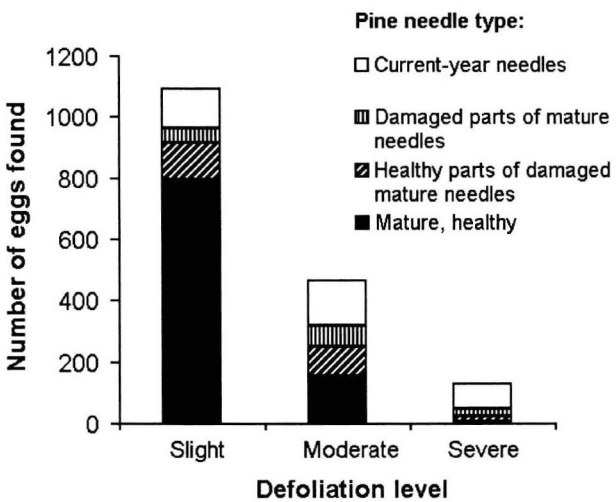

Fig. 3. Number of *B. piniarius* eggs found on different needle types on branches with different level of defoliation.

The egg distribution pattern observed in the field could be the result of several factors, *e.g.* egg predation could be higher on current-year needles than on mature needles. However, a more likely explanation is that current-year needles are not suitable as a egg-laying substrate. *B. piniarius* flight period starts soon after bud burst when current-year needles are actively growing. Because *B. piniarius* females normally deposit eggs in rows on the needle surface, short current-year needles may not be suitable as oviposition substrate. In addition, it may not be safe to oviposit on expanding current-year needles as eggs may be torn from the

rest of the batch and fall to the ground. These arguments formed the basis for the hypothesis that current-year needles are less preferred by ovipositing *B. piniarius* females compared with mature needles.

Additional evidence in support of the preference hypothesis comes from the distribution of eggs within the tree canopy. At endemic population densities *B. piniarius* lays most of the eggs in the upper part of the canopy (Bevan & Brown, 1978). At the defoliated sites at Hökansås eggs tended to be concentrated to the lower branches that were usually less defoliated by *B. piniarius* in the previous year and thus contained more mature needles (III).

Realised fecundity

The absence of a preferred resource may lead to decreased fecundity. For example, populations of the spruce bud moth *Zeiraphera canadensis* decline after tree crown closure because buds on shaded branches are less preferred by ovipositing females then buds on trees in open stands (Ostaff & Quiring, 2000). Similarly, the observed preference for mature needles by ovipositing *Bupalus piniarius* females may result in decreased fecundity when females are confined to only current-year needles. To test this hypothesis laboratory experiments simulating complete defoliation were carried out in the summer of 1998 (III).

B. piniarius females confined to current-year needles were reluctant to lay eggs the first days after emergence. The observed delay in oviposition caused significant reduction in overall realised fecundity. Females confined to current-year needles laid on average 15% less eggs than females on control branches containing both mature and current-year needles. This is in agreement with other studies where females on suboptimal oviposition substrates respond by reduced realised fecundity compared with conspecifics on optimal substrates (Hillyer & Thorsteinson, 1969; Leather *et al.*, 1985). In general, realised fecundity is determined by the interaction between oviposition rate and longevity (Carroll & Quiring, 1993). In this experiment, longevity was not affected by the treatment but at death females on current-year needles contained more fat and slightly more eggs indicating that possibly not all available resources were converted into eggs.

Recruitment success

It was observed that females confined to current-year needles not only responded with reduced fecundity but many eggs were deposited unsafely on needle scales as well as stacked in several rows on top of each other. This was possibly caused by the very short length of current-year needles (1-1.5 cm, compared with 3-4 cm of older needles) at the time of oviposition. Based on the observed misplacement of eggs, and because current-year needles were actively expanding, it was hypothesised that some of the eggs deposited on current-year needles might fall to the ground.

This hypothesis was tested in outdoor experiments in two successive years (III). In 1998, 26.7% of eggs disappeared from current-year needles, and in 1999, 16.2% of the eggs disappeared. No eggs disappeared from mature needles in 1998 and only one single egg disappeared in 1999.

The logical step now was to find out what happen with eggs on the ground. *B. piniarius* larvae are very mobile, and perhaps that they could climb the tall pine trees. However, the neonate larvae hatching on the ground are likely to experience multiple hazards, *e.g.* predation, starvation. Laboratory experiments showed that most of the neonate larvae without food survive no longer than 66 hours and no larvae survive more than 120 hours (III). Furthermore, field experiments revealed that only a small proportion of larvae hatching close to the tree trunk were able to recolonise pine trees (Fig. 4) (III). A similar fate of larvae hatching from fallen eggs is described from other insects (*e.g.* Balbyshev & Lorentzen, 1997).

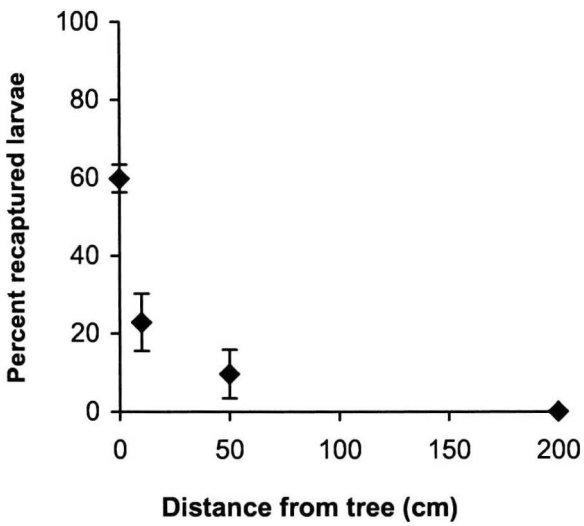

Fig. 4. Percentage (mean ± SE) of newly hatched *Bupalus piniarius* larvae recolonising pine trees from eggs hatching on the ground. Eggs were placed at 0, 10, 50, and 200 cm (n = 4, 3, 3, and 7 larval cohorts respectively) from a trapping tree, and larvae were allowed to search for 48 h (cohorts contained 61 to 247 larvae).

Weather effects on fecundity and fertility

In outbreak situations forest managers may attempt to forecast trends in *Bupalus piniarius* population changes based on a number of parameters, *e.g.* number of owervintering pupae, parasitism rate, size of female pupae (predictor of fecundity) (*e.g.* Apel & Draeger, 1990). Even short periods of adverse weather conditions, however, may significantly affect realised fecundity if females fail to lay all their eggs (Greenfield & Karandinos, 1976), and thus make forecasts unreliable.

Effects of low temperature

Because a slight delay in oviposition can cause a decrease in overall realised fecundity (see above) it was hypothesised that a short period (four days) of low temperature (10 °C) would also cause reduction in fecundity. This hypothesis was tested in laboratory experiments (IV).

A temperature of 10 °C almost completely arrested *Bupalus piniarius* oviposition. Realised fecundity decreased significantly when females were confined to such temperatures for four days after emerging, compared with females experiencing a constant temperature of 20 °C (further referred to as normal temperature). The effect was weaker, when prior to experiencing low temperature females were allowed to oviposit on pine needles for two days at 20 °C. Females confined to low temperatures for four days lived on average three days longer than females experiencing constant optimum temperature. Moreover, females experiencing low temperature had a higher oviposition rate when temperature returned to optimum than females at constant normal temperature. Such compensatory behaviour after unfavourable conditions has been observed in other Lepidoptera (*e.g.* Kehat & Gordon, 1975). However, neither longer longevity nor compensatory oviposition rate was enough to compensate for oviposition arrestment at low temperature.

Delayed mating

In association with bad weather *B. piniarius* females may experience delayed mating. It was hypothesised that delayed mating can result in a reduction in fecundity similar to that at low temperature. In the laboratory experiment it was found that number of eggs laid did not differ between females experiencing a four day delay in mating and females mated at emergence (IV). However, at normal temperature virgin females laid a significant proportion of eggs (30%) before mating. Unfertilised *B. piniarius* eggs do not develop into larvae. Under field conditions delayed mating is more likely to occur at low temperatures when flight is inhibited. However, as female oviposition is arrested at low temperatures, delayed mating does not result in reduced fertility.

Host plant defoliation and possible consequences to *B. piniarius* population dynamics

In this section I summarise processes studied and results obtained in this thesis (Fig. 5). High population densities are associated with crowding and defoliation. I hypothesised that in the build-up phase of an outbreak additive negative effects of crowding and preferred resource depletion will contribute to a reduction of population growth rate. Surprisingly, and contrary to earlier reports (Gruys,

1970) larval performance was enhanced in crowded conditions. In the year following complete defoliation *B. piniarius* may encounter induced responses in the host plant, in addition to the absence of the preferred resource of mature needles. As predicted, confinement to the non-preferred resource had negative effects on larval performance as well as on realised fecundity and egg loss. However, delayed induced responses in pine needles were different from what I expected; instead of induced resistance, defoliated trees showed induced susceptibility. It is likely that any induced resistance was ameliorated by substantially elevated nitrogen levels in current-year needles of defoliated trees (II).

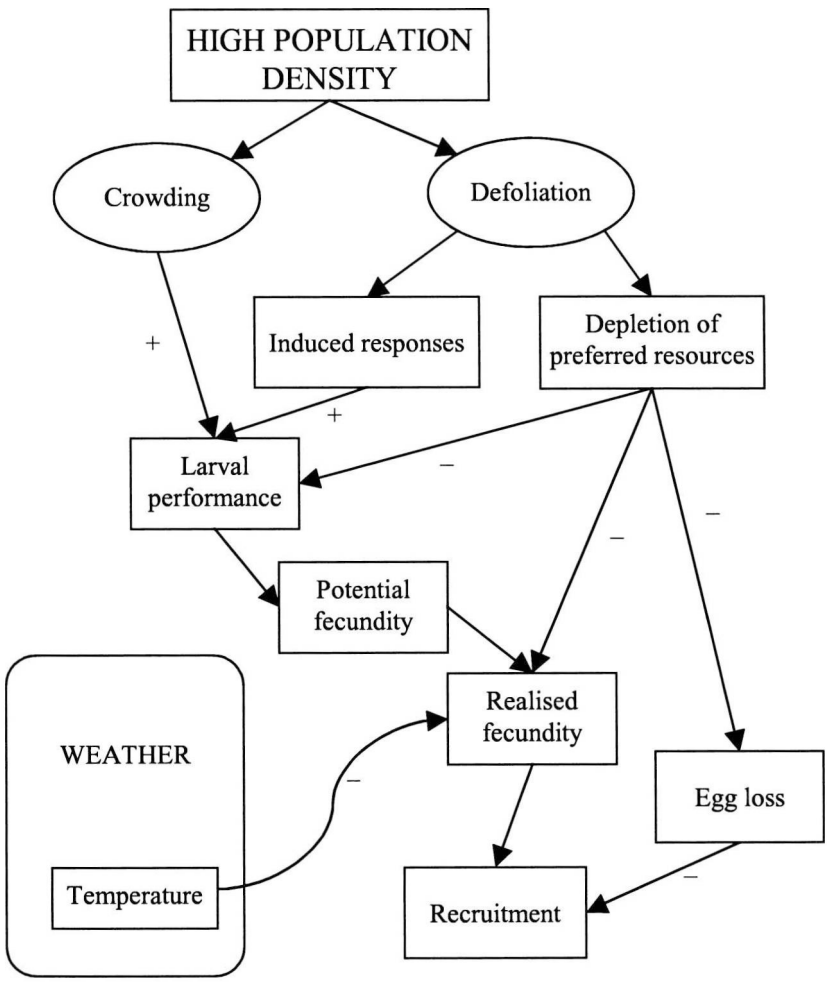

Fig. 5. Conceptual model of processes involved in population dynamics of *Bupalus piniarius* that were studied in this thesis. '+' or '-' indicate positive or negative effects found in the studies.

Pupal weight determines female potential fecundity in *B. piniarius*. However, because foliage affected by defoliation is not only food for larvae but also substrate for oviposition, it is possible that recruitment of the new generation deviates substantially from potential fecundity in defoliated stands. This study showed that realised fecundity is negatively affected by the absence of preferred resources (III). It also showed that some eggs laid on current-year needles fall from the needles and therefore do not develop into larvae (III). Effects of food quality may interact with other factors, *e.g.* prolonged development time on non-preferred resources may lead to higher mortality caused by predation (*e.g.* Häggström & Larsson, 1995). The logical next step towards solving the mysteries behind the re-occurring outbreaks of *B. piniarius* would, therefore, be to study interactions over three trophic levels (*cf.* Larsson *et al.* 2000).

Although a number of ecological studies on *B. piniarius* give us good tools to forecast trends in population change (*e.g.* Apel & Draeger, 1990) random weather events may cause even the best forecasts to become unreliable. Giving insight into such weather effects it was shown that even short periods of low temperature may significantly affect realised fecundity (IV). Day temperatures around 10 °C are occasionally observed in central Sweden at the time of *B. piniarius* peak flight, and precision of forecasts may thus depend on occurrence and duration of time periods with such temperatures.

Summarising effects described above it is evident that defoliation-mediated variation in host plant quality can significantly contribute to *B. piniarius* population dynamics at outbreak conditions. Positive effects on *B. piniarius* performance associated with host plant susceptibility were rather weak compared with negative effects on depletion of preferred resources. Enhanced growth in crowded conditions is unlikely to compensate overall negative effects of plant quality at the outbreak conditions. Finally, this thesis is one of only a few that has addressed defoliation effects on recruitment; effects on realised fecundity and egg survival were of a magnitude likely to significantly modify population growth.

Acknowledgements

I am deeply in dept to my supervisor Stig Larsson. He gave me a serenity to do things that are doable and stay with two feet on the ground. At the same time, his great theoretical knowledge was immense support for planning, doing, and writing research. Still he always left the 'window' for me to challenge my own research approach. Stig always found the time whenever I needed it for discussion, for reading my drafts, even personal problems. I am thankful for his endless patience working with me.

This thesis would never have reached the current form without a great contribution from Barbara Ekbom, Christer Björkman, Helena Bylund, Richard Hopkins, Carolyn Glynn, Toomas Tammaru, Julia Kornicheva, Pekka Niemelä and the late David Tilles to the manuscripts.

My special thanks to my wife Baiba and sons Atis, Reinis, and Matīss for their support of my work with patience and love. My parents in law Anna and Jānis Veide took care of my kids during the long months I have been away from home.

I am grateful to Nico and Britta Wiersma for sharing wonderful times with me and my family. I am thankful to Margit, Ulf and Else-Marie Bertilsson for field accommodation at Hökensås, where I spent a wonderful summer. I also thank Peter Dalin, Peter Zonneveld, Karin Eklund and Ilze Vilks for assistance in the field and laboratory and making fieldwork more fun.

There are many persons who made may stay in Sweden enjoyable. My Latvian colleagues Māris Bisnieks, Olga Vinnere, and Daiga Siļķe did not let me forget my mother language. Richard Hopkins was a great pal and good teacher for my English. I enjoyed chatting at coffee breaks with Peter Dalin, Jan Cedervind, Åke Lindelow, and many others at the department.

People at 'Silava' gave inspiration to continue my work. Jānis Donis, Laila Šica and Ilze Vilks were people that bridged SLU and 'Silava'. I thank director Imants Baumanis for assisting in all possible ways. I am grateful to the big boss Otto Žvagiņš at the Latvian State Forest Service, my current employer, for being so understanding.

There are many more people whom I owe a credit for this thesis. Those I forgot to mention here should think that I thank you anyway.

Many thanks to the Royal Swedish Academy of Science and the C.F. Lundström Foundation whose financial support made this project possible.

This thesis is dedicated to memory of my father Sigurds Šmits. His incredible personality inspired me to step on the road of science.

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